TIMBER RATTLESNAKES AND LOUISIANA PINE SNAKES OF THE WEST GULF COASTAL PLAIN: HYPOTHESES OF DECLINE

D. Craig Rudolph and Shirley J. Burgdorf

Wildlife Habitat and Silviculture Laboratory (Maintained in cooperation with the College of Forestry, SFASU) Southern Research Station, USDA Forest Service Nacogdoches, Texas 75962

Abstract.—Timber rattlesnakes (Crotalus horridus) and Louisiana pine snakes (Pituophis melanoleucus ruthveni) are large-bodied snakes occurring on the West Gulf Coastal Plain. Both species are thought to be declining due to increasing habitat alteration. Timber rattlesnakes occur in closed canopy hardwood and pine-hardwood forests, and Louisiana pine snakes in pine forests on sandy, well drained soils. While various factors are probably involved in population declines, this study examined one factor for each species that may have widespread consequences for population viability. Results obtained in this study support the premise that timber rattlesnakes are vulnerable to mortality associated with roads and vehicular traffic. Data and discussion are presented suggesting that populations are negatively impacted in areas of eastern Texas having a high road density. Conversely, Louisiana pine snakes appear to be affected by changes in the fire regime which has altered vegetation structure resulting in decreases in pocket gopher (Geomys breviceps) density. Decreases in gopher densities are further hypothesized to result in decrease or extirpation of pine snake populations.

Timber rattlesnakes (*Crotalus horridus*) and Louisiana pine snakes (*Pituophis melanoleucus ruthveni*) are large-bodied snakes with low reproductive rates. Thus, they are vulnerable to population decreases due to habitat modifications and increased mortality rates. Anecdotal evidence suggests that both species are declining on the West Gulf Coastal Plain (Conant 1956; Young & Vandeventer 1988; Brown 1991). Consequently, the Texas Parks and Wildlife Department has listed the timber rattlesnake as threatened and the Louisiana pine snake as endangered in Texas (TPWD 1992). In an effort to understand the biology of these two species and elucidate factors that are potentially responsible for the presumed population declines, radio-telemetry studies of both species were initiated.

Both species are undoubtedly subject to a variety of human induced impacts that have reduced populations and resulted in extirpation of local populations. However, this study focuses upon two hypotheses, one for each species, that the authors suspect are of importance in causing

Snake	Minimum Convex Polygon	Harmonic Mean 95% Contour	
TX 1 (male) 1993	105.4	123.7	
TX 1 (male) 1994	113.6	148.8	
TX 2 (male)	212.6	256.7	
TX 3 (female)	19.5	22.1	
TX 4 (female)	20.2	15.3	

Table 1. Annual home range size (ha) of adult timber rattlesnakes in eastern Texas.

declines on a landscape level.

Timber rattlesnake ecology.—Timber rattlesnakes on the Gulf Coastal Plain are typically associated with hardwood and mixed pine-hardwood forests (Martin 1992). Extensive areas dominated by longleaf pine (Pinus palustris) are generally not occupied (Mount 1975; Dundee & Rossman 1989). This general pattern is consistent with observations made in eastern Texas during this study.

Timber rattlesnakes are classic ambush predators, often spending up to several days in a given position waiting for prey to pass within striking distance. Foraging snakes frequently assume positions adjacent to logs, tree trunks or other structures that may be used as travel corridors by prey species (Reinert et al. 1984; Brown & Greenberg 1992). Juveniles occasionally climb trees to heights of 15 m, and may remain in trees for several days (Saenz et al. 1996). Prey typically consists of small mammals up to the size of squirrels (*Sciurus* spp.) and rabbits (*Silvalagus* spp.) (Klauber 1956).

Preliminary radio-telemetry results document the large home ranges of adult male timber rattlesnakes in eastern Texas (Table 1). Adult females have substantially smaller home ranges. The average annual home range size (Harmonic Mean 95% contour) for adult females (19 ha) is much smaller than that of adult males (176 ha). Juvenile snakes have generally smaller home ranges than adult females. The difference in home range size between adult females and adult males is primarily due to differences in movement patterns associated with breeding activities.

Table 2.	Average daily	distance	moved	(m) by	adult	male	and	female	timber	rattlesnakes
during	the mating an	d non-ma	ting sea	son.						

Snake	Non-mating (1 Mar15 Aug)	Mating (16 Aug1 Nov.)	
TX 1 (male) 1993	27.2	71.0	
TX 1 (male) 1994	31.5	59.8	
TX 2 (male)	25.0	85.6	
TX 3 (female)	10.3	18.3	
TX 4 (female)	17.7	15.9	

Based on observations of pairs in close association, actual mating, and movement patterns, the mating season of timber rattlesnakes in eastern Texas is from mid-August until movement to the hibernacula, generally late October to November. A marked change in movement patterns of adult males, but not adult females, occurs at the initiation of the breeding season. Prior to the breeding season adult snakes move relatively short distances and spend extensive periods, often several days, at a given location. Females continue this behavior throughout the active season. This pattern is presumably driven by the ambush predation strategy employed by this species (Reinert et al. 1984).

Commencing with the initiation of the mating season, the movement patterns of adult males change dramatically. Throughout the mating season adult males move more frequently and move longer distances than adult females, or adult males prior to the mating season. This pattern is documented by the average distances moved per day by males and females prior to, and during the mating season (Table 2). Based on approximately once per week telemetry locations of individuals, males move substantially greater distances during the mating season than prior to the mating season (72.1 vs 27.9 m per day). Females' movement distances do not differ substantially between these two periods (17.1 vs 14.0 m per day). This behavior of adult males during the mating season results in movements of 1-2 km per week, traversing loops up to 2 km in diameter.

Causes of mortality and population decline.—Many factors undoubtedly contribute to mortality and population declines of timber rattlesnakes (Brown 1993). Factors associated with human development have pre-

sumably had a detrimental impact on timber rattlesnake populations, especially in recent decades (Brown 1993).

Habitat alteration due to changes in land use patterns have had a generally negative impact on timber rattlesnake populations throughout their range. Urbanization and agricultural development have eliminated the species from much of its historic range (Brown 1993). In eastern Texas urbanization is not as extensive as in some areas, and agriculture (pasture and row crops) have declined in recent decades. Commercial timber production lands are subject to harvesting-related disturbances, often on short rotations, that have unknown impacts on timber rattlesnake populations.

Anecdotal evidence suggests that direct killing by humans is substantial on the West Gulf Coastal Plain, but data are lacking. Rattle-snake roundups, important sources of mortality for some rattlesnake populations, probably have little impact on timber rattlesnake populations in Texas due to legal protection and the difficulty of collection compared to other rattlesnake species. Most human-related mortality reported to the authors is associated with timber harvest activities, incidental encounters during various outdoor activities, and especially with snakes encountered on roads.

Northern populations are subject to massive mortality through direct killing by humans at communal hibernacula (Galligan & Dunson 1979; Brown 1993). Mortality at the den sites is higher on adult females due to the tendency of gravid females to remain in the den vicinity during gestation (Brown 1991). In eastern Texas typical hibernacula consist of armadillo (Dasypus novemcinctus) burrows, decayed stump holes and associated root channels, and beneath the root masses of wind tilted trees. No instances of more than one individual at a hibernation site was observed during this study. Consequently, hibernating rattlesnakes in eastern Texas are not particularly vulnerable to human predation at their hibernacula.

The road mortality hypothesis.—Road networks and substantial vehicle traffic are significant causes of vertebrate mortality (Ehmann & Cogger 1985; Bennett 1991). In the United States Lalo (1987) estimated vertebrate mortality on roads at one million individuals per day. Rattlesnakes are particularly susceptible to road associated mortality since they suffer

from intentional killing due to their economic value and humans' general negative opinions of snakes (Adams et al. 1994).

Encounters between timber rattlesnakes and humans in eastern Texas frequently occur on roads. Of 36 individuals recorded in that study, 16 were of snakes crossing or dead on roads.

Aspects of timber rattlesnake biology influence the patterns of road associated mortality. Human encounters with timber rattlesnakes in eastern Texas, in general and on roadways, are more frequent in late summer and fall. This corresponds with the mating season, suggesting that the increased movements of adult males during this period are responsible for this pattern. Of 21 individuals of known sex recorded by the authors from roads during a three year period, 15 were adult males. This pattern is a potential cause of the skewed sex ratio in favor of adult females at the radio-telemetry study site. Although the sample size is small, adult females captured to date greatly outnumber adult males (8 females, 2 males).

Recent records of timber rattlesnakes were obtained from an 18 county area in eastern Texas. These records indicated that their distribution in the region is primarily associated with the floodplains and adjacent uplands of rivers and permanent streams. Preliminary radiotelemetry results indicate that the snakes are primarily using the uplands adjacent to floodplain habitats. Extensive areas of similar upland habitat not adjacent to rivers and permanent streams currently support few timber rattlesnakes. Differences in density of roads show a similar pattern; i.e., road networks are most dense in the upland areas not adjacent to permanent rivers and streams.

These observations suggest that timber rattlesnakes were more widespread on the landscape in the recent past. It is therefore proposed that development of dense road networks and associated vehicular traffic have resulted in the extirpation or major reduction in timber rattlesnake populations over much of the eastern Texas landscape.

This hypothesis was tested by comparing total lengths of roads within 2 and 4 km of recent rattlesnake locality records with random points. This analysis was first accomplished for the entire 18 county area in eastern Texas. It is possible that timber rattlesnakes are always

Table 3. Total road lengths (km) within 2 and 4 km of all snake collection points and random points, and snake collection points and random points within 3 km of permanent streams.

	Snake Points	Random Points	Prob.
All Points	-		
Total Roads w/in 2 km	4.09	7.01	t = -8.94 P < 0.0001
Total Roads w/in 4 km	13.43	21.44	$t = -2.68 \\ P < 0.0088$
Points w/in 3 km of Permanent Streams			
Total Roads w/in 2 km	4.20	7.82	t = -3.87 P < 0.0003
Total Roads w/in 4 km	13.22	23.70	t = -6.78 P < 0.0001

restricted to forested habitats adjacent to rivers and permanent streams, although the preliminary radio-telemetry results suggest otherwise. To avoid the necessity of the assumption that timber rattlesnakes were once widespread on the eastern Texas landscape, the data was reanalyzed restricting consideration to the subset of the data (snake locations and controls) located within 3 km of rivers and permanent streams. In both analyses (Table 3) a highly significant relationship was found. Recent timber rattlesnake locations have a lower density of roads within 2 and 4 km than do random points. These results support the hypothesis that development of dense road networks and resulting vehicular traffic have significantly reduced timber rattlesnake populations in eastern Texas.

Louisiana pine snake ecology.—The Louisiana pine snake is possibly the least understood of any large snake of the United States due to their limited range, extreme rarity and secretive behavior. They are large, semi-fossorial constrictors with a range restricted to eastern Texas and western Louisiana (Conant 1956). Louisiana pine snakes are generally associated with open pine forests, especially longleaf pine (Pinus palustris), and sandy, well drained soils (Young & Vandeventer 1988). An association with pocket gophers (Geomys breviceps) is frequently noted in the literature (Young & Vandeventer 1988; Sweet & Parker 1991). Data derived from captive breeding programs indicates a remarkably small clutch size (3-4), the lowest of all the subspecies of Pituophis melanoleucus (Reichling 1990).

Preliminary results of on-going radio-telemetry studies in Louisiana and Texas indicate a moderate home range size averaging 27.7 hectares. In the pine upland habitats dissected with a network of small drainages, pine snake activity is heavily concentrated on the low broad ridges overlain with sandy well drained soils. Vegetation typically consists of a pine overstory with moderate to sparse midstory, and a well developed herbaceous understory dominated by grasses.

An extremely close association with pocket gophers is supported by observations made during the course of this study. The distribution of Louisiana pine snakes on the landscape, concentration on sites with sandy well drained soils, matches that of pocket gophers (Davis et al. 1938; Sulentich et al. 1991). Most Louisiana pine snake telemetry locations (approximately 90% of 500 + records) are of snakes in or immediately adjacent to pocket gopher burrow systems. Individuals disturbed on the surface frequently retreat to nearby pocket gopher burrows. In addition, all hibernation sites located to date (n = 27) have been in pocket gopher burrow systems. Finally, Louisiana pine snakes are thought to prey heavily on pocket gophers (Vandeventer & Young 1989).

Causes of mortality and population decline.—Louisiana pine snake populations are thought to have declined in recent decades (Jennings & Fritz 1983; Young & Vandeventer 1988; Reichling 1995). Lack of baseline population data, rarity, and secretive behavior make any conclusions speculative. Intensive trapping efforts conducted during this study within the historic range suggest that current populations are very low with local pockets of higher density.

Louisiana pine snake populations are subject to many of the impacts common to other large snake species. Speculation in the literature as to causes of decline has included habitat alteration, direct human predation, collection for the pet trade and road mortality (Young & Vandeventer 1988). Data are lacking to evaluate the relative impacts of these potential causes of population decline.

Alteration of the fire regime hypothesis.—Most of the historic range of the Louisiana pine snake is still forested. However, essentially the entire historic range has been extensively altered by forestry practices (Frost 1993; Outcalt & Outcalt 1994). All but a few hectares of the

original pine forests of the region have been harvested at least once. Most of the original longleaf pine habitat has been converted to other pine species, primarily loblolly pine (*Pinus taeda*) and slash pine (*P. elliottii*), due to alteration of the fire regime or direct planting. Rotation ages under current silvicultural practices preclude the regeneration of old growth forests, and short rotation silviculture for pulp production is dominant on private lands.

The impact of these habitat alterations on Louisiana pine snake populations is not known. Studies currently in progress are designed to answer questions concerning habitat use in relation to silvicultural practices. What is obvious from preliminary data is the close association of these snakes with pocket gophers. It is therefore hypothesized that factors that influence pocket gopher distribution and abundance also influence Louisiana pine snake distribution and abundance, specifically that pocket gopher declines precipitate Louisiana pine snake declines. It is further proposed that the distribution and abundance of pocket gophers is determined in part by the fire regime, and that changes in the historic fire regime have had a negative impact on pocket gopher abundance.

West Gulf Coastal Plain pine forests, especially longleaf pine, have evolved as fire climax communities due to effects of frequent, low intensity ground fires (Komarek 1964; Platt et al. 1988). Frequently burned sites on sandy, well drained soils typically support a pine dominated overstory, minimal midstory, and a well developed herbaceous understory (Bridges & Orzell 1989). Alteration of the historic fire regime has been widespread (Frost 1993). Fire suppression has reduced the frequency of fire, and the substitution of prescribed fire for wildfire has changed the seasonal occurrence. The result has been a widespread encroachment of woody vegetation forming a dense midstory, and the suppression or virtual elimination of the previously well developed herbaceous understory (Frost et al. 1986; Bridges & Orzell 1989).

Pocket gophers feed primarily on subterranean portions of herbaceous plants (English 1932; Sulentich et al. 1991). The widespread decline of herbaceous vegetation in West Gulf Coastal Plain pine communities has presumably reduced pocket gopher abundances. Although there may be problems with this approach (Andersen 1987), this study used pocket gopher mound densities as an index of pocket gopher abundance. Pre-

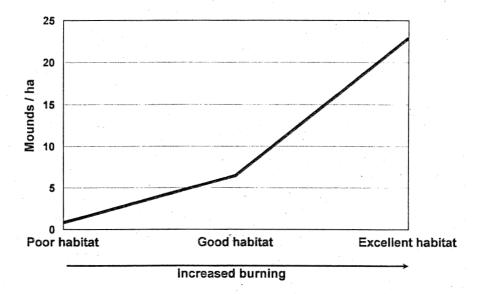


Figure 1. Hypothesized relationship between effectiveness of burning and pocket gopher (Geomys breviceps) density based on preliminary data on mound density.

liminary data suggest that habitats that have a vegetation structure typical of fire climax conditions (well developed herbaceous stratum) support higher gopher densities than sites where fire has not been sufficient to suppress woody vegetation and prevent reduction of the herbaceous stratum (Fig. 1).

Further confirmation of the relationship between pocket gopher densities and the fire regime would support the hypothesis that pocket gopher population declines in West Gulf Coastal Plain pine habitats have resulted in the apparent decline of Louisiana pine snake populations.

CONCLUSIONS

Two hypotheses have been presented for the apparent population declines of two large snake species on the West Gulf Coastal Plain. The first is that development of a dense road network and associated vehicular traffic have led to the elimination or decline of timber rattlesnake populations throughout the region. In the case of Louisiana pine snakes,

it is proposed that changes in the fire regime have reduced pocket gopher densities and thereby led to a decline in pine snake populations. Preliminary data were discussed to test these two hypotheses. Hopefully, additional data will be forthcoming to critically test these hypotheses.

ACKNOWLEDGMENTS

The authors wish to thank Robert R. Fleet, James A. Neal, Ronald E. Thill, Daniel Saenz and two anonymous reviewers for commenting on earlier drafts of this manuscript. The U.S. Fish and Wildlife Service, Texas Parks and Wildlife Department and the Louisiana Department of Game and Fisheries provided funding for the research on *Pituophis* under Section 6 of the U.S. Endangered Species Act. Texas Parks and Wildlife Department issued the necessary scientific collecting permits.

LITERATURE CITED

- Andersen, D. C. 1987. *Geomys bursarius* burrowing patterns: influence of season and food patch structure. Ecology, 68:1306-1388.
- Adams, C. E., J. K. Thomas, K. J. Strnadel & S. L. Jester. 1994. Texas rattlesnake roundups: implications of unregulated commercial use of wildlife. Wildl. Soc. Bull., 22:234-330.
- Andersen, D. C. 1987. Geomys bursarius burrowing patterns: influence of season and foodpatch structure. Ecology, 68:1306-1318.
- Bennett, A. F. 1991. Roads, roadsides and wildlife conservation: a review. Pp. 99-118 in Nature Conservation II: The role of Corridors (D. A. Saunders & R. J. Hobbs, eds.). Surrey Beatty & Sons, Heidelberg, Victoria, Australia, 442 pp.
- Bridges, E. L. & S. L. Orzell. 1989. Longleaf pine communities of the West Gulf Coastal Plain. Natural Areas Journal, 9:246-253.
- Brown, W. S. 1991. Female reproductive ecology in a northern population of the timber rattlesnake, *Crotalus horridus*. Herpetologica 47:101-115.
- Brown, W. S. 1993. Biology, status, and management of the timber rattlesnake (*Crotalus horridus*): a guide for conservation. Society for the Study of Amphibians and Reptiles. Herpetological Circular No. 22.
- Brown, W. S. & D. B. Greenberg. 1992. Vertical-tree ambush posture in *Crotalus horridus*. Herpetol. Rev., 23:67.
- Conant, R. 1956. A review of two rare pine snakes from the Gulf coastal plain. Amer. Mus. Novitates, 1781:1-31.
- Davis, W. B., R. R. Ramsey & J. M. Arendale, Jr. 1938. Distribution of pocket gophers (*Geomys breviceps*) in relation to soils. J. Mammology, 19:412-418.
- Dundee, H. A. & D. A. Rossman. 1989. The amphibians and reptiles of Louisiana. Louisiana State Univ. Press, Baton Rouge, Louisiana, 300 pp.

- Ehmann, H. & H. Cogger. 1985. Australia's endangered herpetofauna: a review of criteria and policies. Pp. 435-437 in Biology of Australian Frogs and Reptiles (G. Gregg, R. Shine, & H. Ehmann, eds.). Surrey Beatty & Sons, Sydney, New South Wales, Australia, 527 pp.
- English, P. F. 1932. Some habits of the pocket gopher, Geomys breviceps breviceps. J. Mammalogy, 12:253-256.
- Frost, C. C. 1993. Four centuries of changing landscape patterns in the longleaf pine ecosystem. Proc. of the Tall Timbers Fire Ecology Conf. 18:17-43.
- Frost, C. C., J. Walker & R. K. Peet. 1986. Fire dependent savannas and prairies of the Southeast: original extent, preservation status and management problems. Pp. 348-357 in Wilderness and Natural Areas in the Eastern United States: a Management Challenge (D. L. Kulhavy & R. N. Conner, eds.). Center for Applied Studies, School of Forestry, Stephen F. Austin State Univ., Nacogdoches, Texas, 416 pp.
- Galligan, J. H. & W. A. Dunson. 1979. Biology and status of timber rattlesnake (*Crotalus horridus*) populations in Pennsylvania. Biol. Conserv., 15:34-28.
- Jennings, R. D. & T. H. Fritz. 1983. The status of the black pine snake Pituophis melanoleucus lodingi and the Louisiana pine snake Pituophis melanoleucus ruthveni. U. S. Fish and Wildl. Serv. and the Univ. of New Mexico Mus. of Southwestern Biol. pp 1-32.
- Klauber, L. M. 1956. Rattlesnakes: their habits, life histories, and influence on mankind. University of California Press, Berkeley, California, 1533 pp.
- Komarek, E. V. 1964. The natural history of lightning. Proc. of the Tall Timbers Fire Ecology Conf., 3:139-183.
- Lalo, J. 1987. The problem of roadkill. American Forests 50:50-52.
- Martin, W. H. 1992. The timber rattlesnake: Its distribution and natural history. Pp. 13-22 in Conservation of the timber rattlesnake in the northeast (T. F. Tyning, ed.). Massachusetts Audubon Society, Lincoln, Massachusetts, 40 pp.
- Mount, R. H. 1975. The reptiles and amphibians of Alabama. Auburn Univ. Agri. Exp. Sta., Auburn, Alabama.
- Outcalt, K. W. & P. A. Outcalt. 1994. The longleaf pine ecosystem: an assessment of current conditions. Unpubl. report on USDA Forest Service Forest Inventory and Analysis Data. 23 pp.
- Platt, W. J., G. W. Evans, & S. L. Rathbun. 1988. The population dynamics of a long-lived conifer (*Pinus palustris*). Amer. Naturalist 131:491-525.
- Reichling, S. B. 1990. Reproductive traits of the Louisiana pine snake *Pituophis melanoleucus ruthveni* (Serpentes: Colubridae). SW Naturalist, 35:221-222.
- Reichling, S. B. 1995. The taxonomic status of the Louisiana pine snake (*Pituophis melanoleucus ruthveni*) and its relevance to the evolutionary species concept. J. Herpetology, 29:186-198.
- Reinert, H. K., D. Cundall & L. M. Bushar. 1984. Foraging benhavior of the timber rattlesnake, *Crotalus horridus*. Copeia 1984:976-981.
- Saenz, D., S. J. Burgdorf, D. C. Rudolph & C. M. Duran. 1996. Crotalus horridus (timber rattlesnake). Climbing. Herpetol. Rev., 27:145.
- Sulentich, J. M., L. R. Williams & G. N. Cameron. 1991. Geomys breviceps. Mammalian Species, 383:1-4.
- Sweet, S. S. & W. S. Parker. 1991. Pituophis melanoleucus. Catalogue of American Amphibians and Reptiles, 474:1-8.
- TPWD. 1992. Texas threatened and endangered species. Texas Parks and Wildlife Department, Austin, Texas, 4 pp.

Young, R. A. & T. L. Vandeventer. 1988. Recent observations on the Louisiana pine snake, *Pituophis melanoleucus ruthveni*, Stull. Bull Chicago Herp. Soc., 23:203207.